

# Revision and supplementary note on Miocene sciurid fauna of Sihong, China

QIU Zhu-Ding

(Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044  
qiuzhuding@ivpp.ac.cn)

**Abstract** The Sihong sciurid fauna, a relatively diverse squirrel assemblage found in Jiangsu, China in 1983, is restudied. On the basis of the updated knowledge of Miocene sciurids, the specimens from the Early Miocene Xiacaowan Formation are reexamined and additional descriptions provided, and definitions of the new genera and species previously established are amended. A new genus *Heterotamias* is named based on the material previously assigned to *Eutamias*; *Shuanggouia* formerly placed in Pteromyinae is here considered to be a member of Sciurinae due to its generalized sciurid dental pattern; some specimens previously referred to *Shuanggouia lui* are now identified with *Palaeosciurus* on account of their differences from the holotype of the species. Five species, *Palaeosciurus jiangi*, *Heterotamias sihongensis*, *Plesiosciurus sinensis*, *Shuanggouia lui* and *Parapetaurista tenurugosa*, are recognized in this restudy. Among them, *Parapetaurista* shows similarities to the Middle–Late Miocene *Miopetaurista* in dental pattern, but their systematic relationship remains uncertain. The Sihong squirrels appear to represent a sciurid fauna dominated by chipmunk-like animals and restricted to eastern China.

**Key words** Sihong, China, Early Miocene, Xiacaowan Formation, Sciuridae

## 1 Introduction

Remains of Neogene sciurids in China were not commonly known until 1980s. The Sihong assemblage from the Early Miocene Xiacaowan Formation in Jiangsu Province is one of the relatively diverse sciurid faunas found in this country. A preliminary report on the fauna was given by Li et al. (1983). The material was later described by Qiu and Lin (1986), and assigned to five species in two subfamilies, the Petauristinae *Parapetaurista tenurugosa* and *Shuanggouia lui*, and, *Eutamias sihongensis*, *Plesiosciurus sinensis* and an indeterminate sciurid in Sciurinae. In light of the knowledge gained from the expansion of fossil record and with the enhancement of knowledge of Miocene faunas in China, the previous description and interpretation of the Sihong sciurid association need improvement and revision. In particular, most genera and species described from Sihong were new at that time, and Sihong became the type locality for several species. Diagnosis of these genera and species, obviously, needs

国家自然科学基金(批准号: 41430102)资助。

收稿日期: 2015-02-28

further amending and improving. The purpose of the present paper is to restudy the fauna, including two main objectives: first, to reexamine the specimens of the collection and modify the description published before; and second, to clarify the systematic position of the taxa assigned by earlier workers to the Sciuridae. For the geological background of the localities producing the remains and the measurements of the specimens, the reader is referred to Li et al. (1983) and Qiu and Lin (1986).

## 2 Systematic description

### Sciuridae Gray, 1821

#### Sciurinae Fischer von Waldheim, 1817

#### *Palaeosciurus* Pomel, 1853

#### *Palaeosciurus jiangi* sp. nov.

(Fig. 1)

*Miopetaurista* sp. II: Li et al., 1983, p. 313, partim

*Shuanggouia lui*: Qiu and Lin, 1986, p. 198, partim

*Sciurus lii*: Qiu and Qiu, 2013, p. 147

**Etymology** Named in honor of Mr. Jiang Zhongjian from the Sihong Cultural Museum, who helped to organize the field works during the field seasons.

**Holotype** Right M1/2 (IVPP V 8154.4 from Shuanggou).

**Paratypes** Two m1/2 (V 8154.5,6 from Shuanggou).

**Referred specimens** Songlinzhuang: six cheek teeth (1 P4, 1 M3, 1 p4, 2 m1/2, 1 m3), V 8154.9, 10, 12, 13, 17, 19. Zhengji: one p4, V 8154.22.

**Diagnosis** Larger-sized *Palaeosciurus*. P4-M2 with slightly constricted protocone, conspicuous mesostyle, protoloph and metaloph distinctly converging towards protocone, undeveloped protoconule and small metaconule; p4-m2 with small but delimited entoconid, strong mesoconid, narrow and shallow notch between entoconid and mesostylid; m1-m3 with complete metalophid. Enamel on basins heavily rugose.

**Description** The P4 is trapezoid in outline of the occlusal surface with a prominent and moderately expanded parastyle. The protocone is large and located slightly anterior to the midline. The protoloph and metaloph are complete and lingually converged to join the protocone. A protoconule is absent, but a metaconule is present. There is a small mesostyle. The enamel of the central valley is wrinkled. The M1/2 is subquadrate in occlusal outline. The protocone is large and slightly constricted anteroposteriorly. The protoloph and metaloph are complete and strong, but constricted just buccal of the protocone, and slightly converge toward the protocone. A tiny protoconule and a small metaconule are present. The mesostyle is rather marked. The M3 is moderately expanded posteriorly. The protoconule is indistinct. A reduced metaloph is present lingually. As the M1/2, the valley shows an irregular pattern of crests.

The p4 is distinctly narrower anteriorly than posteriorly due to the closing of the

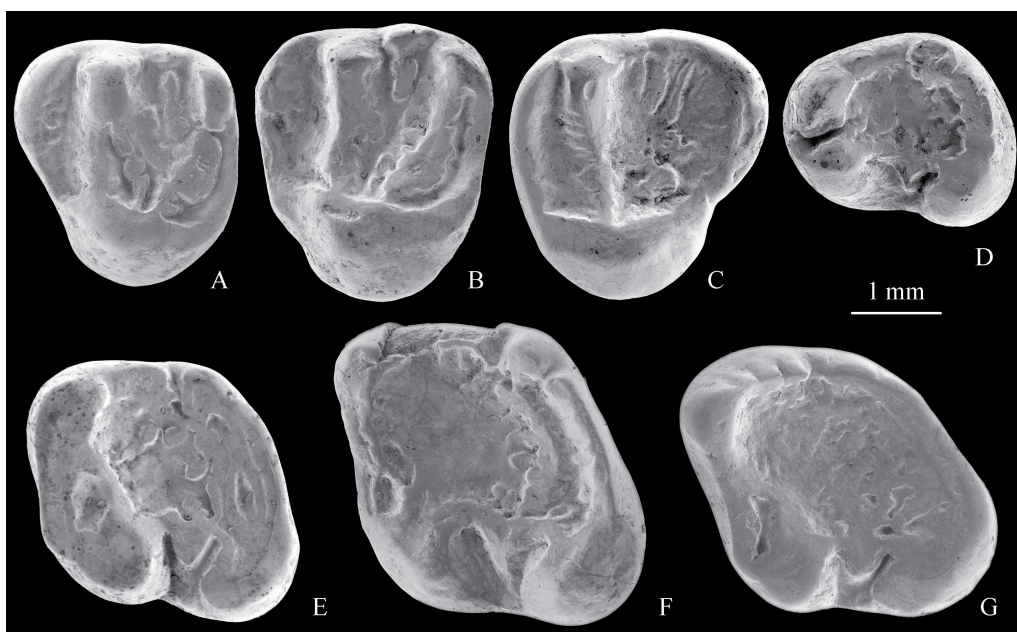


Fig. 1 Cheek teeth of *Palaeosciurus jiangi* from Sihong, Jiangsu in occlusal view  
 A. r P4 (reversed, IVPP V 8154.9); B. r M1/2 (reversed, holotype, V 8154.4); C. l M3 (V 8154.10);  
 D. l p4 (V 8154.22); E. l m1/2 (V 8154.13); F. r m1/2 (reversed, V 8154.6); G. l m3 (V 8154.19)

protoconid and the metaconid. The entoconid is delimited. The mesoconid is distinct. The mesostylid is poorly developed. The m1/2 is subrhomboidal and slightly compressed anteroposteriorly. The entoconid is delimited, connected with the high posterolophid and separated from the weak mesostylid by a shallow notch. The entoconid corner is angular. The mesoconid is distinct. The anterolophid is strong and joins the protoconid. The metalophid is complete or nearly complete. The buccal valley is moderately wide and the talonid basin is dammed by a complete ectolophid. The m3 is weakly expanded posteriorly. The entoconid is incorporated into the posterolingual crest. The mesoconid is rather strong. The metalophid closes the trigonid posteriorly. As the other molars, enamel of the basin is rugged.

**Discussion** The specimens described were previously referred to *Shuanggouia lui*, and later to *Sciurus*, comparing with *S. lii* (Qiu and Lin, 1986; Qiu and Yan, 2005). These teeth are similar to those of *Shuanggouia* in having moderately elevated cusps and crests, high protocone, complete and more or less convergent protoloph and metaloph, a marked metaconule in P4-M2, and a partly incorporated entoconid and a nearly complete metalophid in p4-m2, but differ in the protoloph and metaloph less converging towards the protocone, having a more distinct mesostyle in P4-M2, a delimited entoconid and more prominent mesoconid and mesostylid in p4-m2, and more robustly wrinkled enamel in the basins. Obviously, they do not correspond in all features with the type specimen of *Shuanggouia* from Shuanggou. These specimens show some similarities to *Sciurus lii* from Shanwang in size and in having a less expanded protocone, less convergence of the protoloph and metaloph, and a distinct mesostyle

in P4 and M1/2, and a delimited entoconid, a strong mesoconid and a complete metalophid in p4 or m1/2. Nevertheless, the teeth exhibit some differentiating characters. These characters are the presence of a distinct metaconule in P4 and M1/2, the relatively elongated shape of m1, and the much more robustly wrinkled enamel in the basins. However the Sihong specimens essentially exhibit the diagnosis of *Palaeosciurus* Pomel by their subquadrate M1/2 with protoloph and metaloph converging towards the protocone and slightly constricted at their contact with the protocone, and mesostyle and metaconule present, lower cheek teeth with obvious entoconid separated from the mesostylid by a notch, and distinct mesoconid and mesostylid, m1 and m2 with an angular entoconid corner, rugged enamel on the talonid, and anterolophid connected with the protoconid..

*Palaeosciurus* is considered a group of ground squirrels ranging in the Oligocene to Middle Miocene of Eurasia. Five species, *P. feignouxi*, *P. fissurae*, *P. goti*, *P. sutteri* and *P. ultimus* from the Oligocene and Miocene of Europe are known (Dehm, 1950; Vianey-Liaud, 1974; Ziegler and Fahlbusch, 1986; Mein and Ginsburg, 2002). The Sihong *Palaeosciurus* differs from all the known species, and appears to represent a new form of the genus. The new species *P. jiangi* is slightly larger than *P. fissurae* in size, and differs from the European Oligocene form in having distinctly convergent protoloph and metaloph with pronounced metaconule on M1/2, more prominent mesoconid and more curved entoconid corner on m1/2, and more rugged enamel of the basins. It differs from *P. feignouxi* in having a more pronounced entoconid and mesoconid on m1/2, and more rugged enamel in the basins. *P. jiangi* is easily distinguished from *P. goti* by its much larger size, having slightly constricted protocone, more convergent protoloph and metaloph towards the protocone on M1/2, more developed metalophid on m1/2, and more wrinkled enamel of the basins. The new species is similar to *P. sutteri* in size, having more or less constricted protocone and converging arrangement of protoloph and metaloph on M1/2, in the outline of the occlusal surface of M3, and having prominent mesoconid and complete metalophid on m1/2, but differs from it in having stronger mesostyle on M1/2, less delimited entoconid and mesostylid, and narrower buccal valley on m1/2, and more wrinkled enamel of the basins (see Ziegler and Fahlbusch, 1986; De Bruijn, 1998; Daxner-Höck, 1998, 2003). *P. ultimus* from La Grive-Saint-Alban, France (MN7-8) is the youngest species of the genus, and differs from the Chinese new species in slightly smaller size, having less distinct metaconule on M1/2, more marked notch between the entoconid and mesostylid, and weakly developed metalophid on m1/2, more posteriorly expanded M3 and m3, and indistinctly wrinkled enamel of the basins.

For a long time remains of *Palaeosciurus* were only known in Europe. Until not long ago, they were reported in Asia as an indeterminate species from the Early Miocene of Xinjiang (Meng et al., 2006). *P. jiangi* represents the eastern extension of *Palaeosciurus*.

#### ***Heterotamias* gen. nov.**

**Type species** *Eutamias sichongensis* (= *Heterotamias sichongensis*) Qiu & Lin, 1986.



**Etymology** From Greek *heteros*, “other or different”, alluding to the difference of the new genus from *Tamias*, a genus of chipmunks.

**Diagnosis** Small sized chipmunk. P4 with unexpanded parastyle and long anteroloph; P4-M2 with unexpanded protocone, weakly developed protoconule and distinct metaconule, complete protoloph and metaloph converging towards the protocone and usually distinctly constricted at the contact with the protocone; M3 with metaconule and remnant of metaloph; p4-m2 with pronounced entoconid and obtuse or curved entoconid corner, usually small mesoconid, longitudinal ectolophid, and wide buccal valley; m1 and m2 longer than wide, with long metalophid, and entolophid or its vestige in early wear stage; m3 moderately expanded posteriorly, with more distinct mesoconid, but shorter metalophid than in m1 and m2. Enamel in basins rugged in early stages of wear.

**Differential diagnosis** The dental pattern of *Heterotamias* is similar to that of the generalized sciurids in having simple structure, in lacking of hypocone in M1 and M2, and of hypolophid in m1 and m2. By size the new genus is closer to the small-sized sciurines *Tamias*, *Tamiops*, *Plesiosciurus*, *Sinotamias* and *Prospermophilus*, but is easily distinguished from the larger-sized sciurines of the Neogene, such as *Sciurus*, *Oriensciurus*, *Shuanggouia*, *Atlantoxerus*, and *Palaeosciurus*, etc.

*Heterotamias* differs from *Tamias* in: 1) the P4 has a longer anteroloph; 2) the P4-M2 have weakly developed protoconule and distinct metaconule; 3) the M3 has a metaconule and remnant of metaloph; 4) the entoconid is more prominent in p4-m2; 5) both m1 and m2 are longer than wide, with longer metalophid, and entolophid or its vestige in unworn teeth; 6) enamel in basins is more rugged in early stages of wear.

The main differences between *Heterotamias* and *Tamiops* are: 1) the parastyle in P4 is less pronounced and anteriorly-expanded in *Heterotamias* than in *Tamiops*; 2) the protoconule and metaconule in P4-M2 are much more distinct in *Heterotamias* than in *Tamiops*; 3) the protoloph and metaloph in P4-M2 converge towards the protocone in *Heterotamias*, but in *Tamiops* they are nearly parallel; 4) a distinct metaconule and remnant of metaloph in M3 are present in *Heterotamias*, but in *Tamiops* they are absent; 5) the wide buccal valleys of the talonid basin are dammed by a longitudinal ectolophid usually bearing a small mesoconid in p4-m3 in *Heterotamias*, but in *Tamiops* the valley is narrow, the ectolophid is in anterolingual-posterobuccal direction, and a mesoconid is missing.

Conspicuous differences between *Heterotamias* and *Plesiosciurus* are: 1) the teeth are less heavily built in *Heterotamias* than in *Plesiosciurus*; 2) the protocone in P4-M2 is smaller and less anteroposteriorly expanded in *Heterotamias* than in *Plesiosciurus*; 3) the anteroloph on P4 is longer in *Heterotamias* than in *Plesiosciurus*; 4) the protoconule in P4-M2 is visible in *Heterotamias*, but in *Plesiosciurus* it is completely wanting; 5) the protoconid and metaconid in p4 are less closely arranged in *Heterotamias* than in *Plesiosciurus*; 6) the m1 and m2 are elongated anteroposteriorly in *Heterotamias*, but in *Plesiosciurus* they are compressed; 7) the entoconid is delimited in p4-m2 in *Heterotamias*, but in *Plesiosciurus* it is completely

submerged in the posterolophid.

*Heterotamias* is slightly smaller with less heavily built cusps than *Sinotamias*. Further differences between the two genera are the presence in the former of a longer anteroloph in P4, a metaconule and remnant of metaloph in M3, a distinct entoconid in p4-m2, a reduced entolophid in m1 and m2, and a wide buccal valley in p4-m3 with the talonid basin dammed by the longitudinal ectolophid bearing a small mesoconid, rather than a narrow buccal valley dammed by a posterolingually-curved ectolophid bearing no mesoconid as in *Sinotamias*. In addition, enamel in the basins in *Heterotamias* is rugged in unworn teeth.

*Heterotamias* is similar to *Prospermophilus* in size, but differs from the latter almost in the same characters used to differentiate it from *Sinotamias*. Additionally, the metaloph is more complete and the protoconule is more distinct in P4-M2, and the metalophid is longer in lower molars than in *Prospermophilus*.

*Heterotamias* also shows similarities to some species of *Heteroxerus* in size and in having a reduced metaconule in M3 and an entolophid in m1 and m2, but differs in the absence of a hypocone in upper molars, in having a complete metaloph in M1 and M2, and in lack of a free buccal arm of the anterolophid but a distinct mesoconid in m1 and m2.

### ***Heterotamias sihongensis* (Qiu & Lin, 1986)**

(Fig. 2)

*Sciurus* sp.: Li et al., 1983, p. 313

*Eutamias sihongensis*: Qiu and Lin, 1986, p. 200

*Plesiosciurus sinensis*: Qiu and Lin, 1986, p. 202, partim

*Eutamias sihongensis*: Qiu and Qiu, 2013, p. 147

**Holotype** Right M1/2 (IVPP V 8155 from Songlinzhuang).

**Paratypes** Sixteen cheek teeth (4 M1/2, 2 M3, 1 p4, 6 m1/2, 3 m3 from Songlinzhuang), V 8156.1-16.

**Referred specimens** Shuanggou: five molars (3 M1/2, 1 M3, 1 m1/2), V 8156.17-21. Zhengji: eighteen cheek teeth (2 DP4, 1 P4, 4 M1/2, 3 M3, 1 dp4, 2 p4, 2 m1/2, 3 m3), V 8156.22-38, V 8158.16.

**Diagnosis** Same as for the genus.

**Description** The outline of the occlusal surface of the DP4 is subtriangular, due to the expansion of parastyle. The protocone is small and pointed. The protoloph and metaloph converge towards the protocone. The metaloph bears a small metaconule and is constricted at the contact with the protocone. A tiny, but distinct mesostyle is present. The P4 is similar to the DP4 in structure, but with a less expanded parastyle, longer anteroloph, more lingually constricted protoloph and metaloph, and a weaker mesostyle. The outline of M1/2 is subquadrate. The protocone is small and unexpanded anteroposteriorly. The protoloph and metaloph are complete, converging towards the protocone, but more or less constricted just buccal of the protocone. A protoconule is weakly developed or absent, and the metaconule

is usually pronounced. A tiny mesostyle is present occasionally. The M3 is moderately expanded posteriorly and shows no notch between the posterior arm of the protocone and the posteroexternal lobe. A distinct metaconid and a remnant of metaloph are present. In unworn M3 the basin shows an irregular pattern of crests.

The dp4 is distinctly narrower anteriorly than posteriorly with the protoconid and the metaconid situated very close to one another and separated by a narrow fissure. The entoconid is incorporated in the prominent posterolophid. A mesoconid and a mesostylid are absent. The p4 is similar to the dp4 in shape and structure, except for its larger size, stronger cusps and crests, less anteriorly situated metaconid, weaker mesoconid, and more pronounced entoconid.

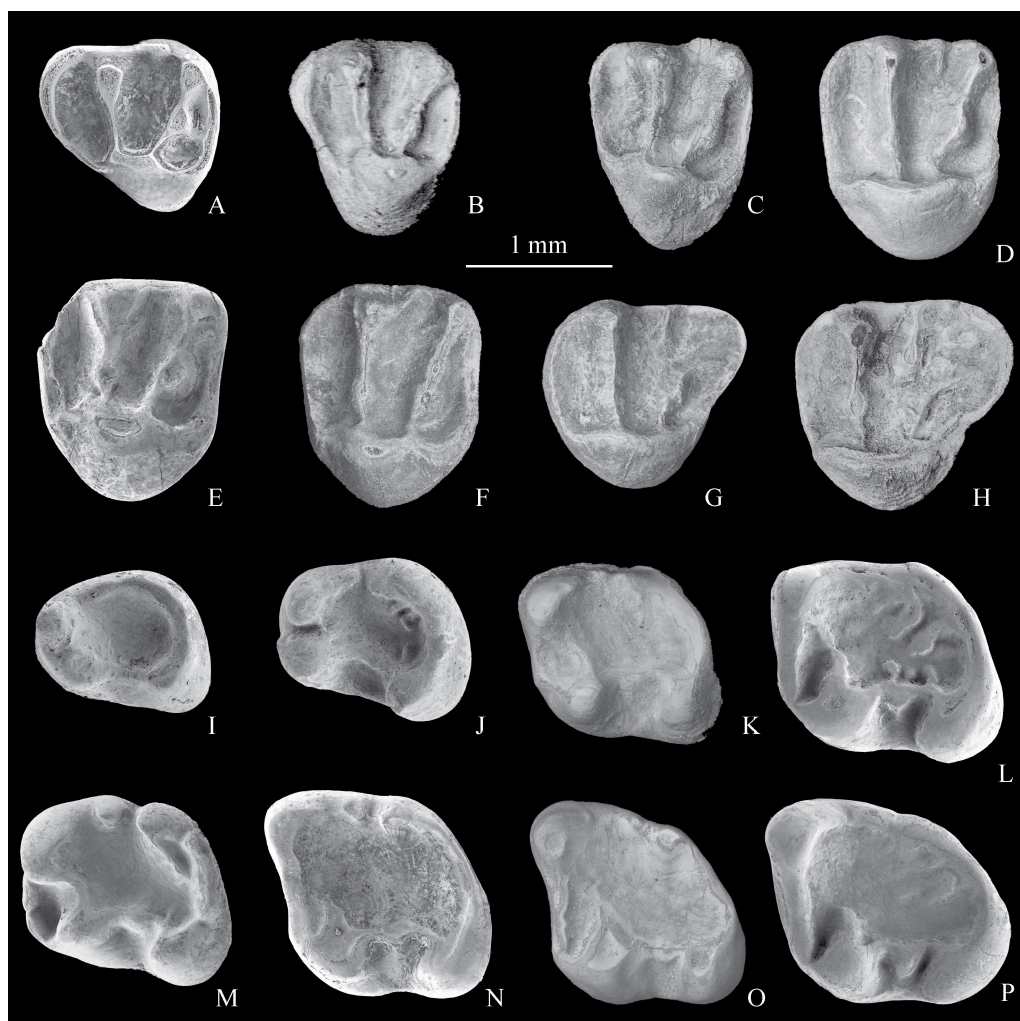


Fig. 2 Cheek teeth of *Heterotamias sihongensis* from Sihong, Jiangsu in occlusal view  
 A. l DP4 (IVPP V 8156.22); B. l P4 (V 8156.24); C. l M1/2 (V 8156.25); D. l M1/2 (V 8156.19); E. r M1/2 (reversed, V 8156.2); F. r M1/2 (reversed, holotype, V 8155); G. l M3 (V 8156.5); H. l M3 (V 8156.29); I. l dp4 (V 8156.32); J. l p4 (V 8156.34); K. l m1/2 (V 8156.8); L. l m1/2 (V 8156.36); M. r m1/2 (reversed, V 8156.21); N. r m1/2 (reversed, V 8156.11); O. l m3 (V 8156.13); P. l m3 (V 8156.38)

The m1/2 is longer than wide. The anteroconid is poorly developed. The entoconid is either partly incorporated in the posterolophid or well delimited. The entoconid corner is obtuse or curved. The mesoconid is variable from distinct to absent. A small and marked mesostylid is usually present, which is connected with the metaconid and separated from the entoconid by a notch. The posterolophid is evidently more elevated than the anterolophid. The metalophid is long and usually closes the trigonid basin posteriorly. An entolophid or its vestige can be observed in lightly worn teeth. The buccal valley is wide and the talonid basin dammed by the complete and nearly longitudinally arranged ectolophid. The m3 is not much expanded posteriorly. The entoconid, though incorporated in the posterolophid, is clearly distinguishable. The mesoconid is relatively larger, and the metalophid is shorter than in the m1/2. As in the m1/2 the anterolophid is connected with the protoconid. Enamel of the talonid basin of p4-m3 is rugged in the early stages of wear.

**Discussion** The described specimens were previously referred to the genus *Eutamias* (Qiu and Lin, 1986). They really exhibit some features of the chipmunks, such as the small dimension, the subquadrate P4-M2 with unexpanded protocone, the complete protoloph and metaloph converging towards the protocone, the lingually constricted metaloph bearing metacone, the rhomboidally outlined m1 and m2 with untypical angular distolingual corner and the anterolophid connecting to the protoconid. However, their characters, such as the long anteroloph of P4, the presence of a weak protoconule and a prominent metaconule in P4-M2, the presence of metaconule and remnant of metaloph in M3, the pronounced entoconid present in p4-m2, the distinctly elongated m1 and m2 with long metalophid and reduced entolophid, seem to suggest that the squirrel represented by these material should be assigned to a new genus different from *Eutamias* or *Tamias*.

In my opinion, these morphological resemblances of *Heterotamias* and *Tamias* may indicate that the two genera were probably closely allied, and they appear to be naturally grouped in one tribe Tamiini. *Heterotamias* and *Tamias* presumably arose from a common ancestor before Miocene, but the former with a short history is not as successful as the latter.

### ***Plesiosciurus* Qiu & Lin, 1986**

**Type species** *Plesiosciurus sinensis* Qiu & Lin, 1986.

**Emended diagnosis** Small sized squirrel with relatively heavily built teeth, and more pronounced cusps than crests. P4 with slightly expanded parastyle and short anteroloph; P4-M2 with moderately expanded protocone, no protoconule and mesostyle but relatively distinct metaconule, thin and complete protoloph and metaloph nearly converging towards the protocone, protoloph slightly bulging just buccal of the protocone, and metaloph greatly constricted at the base of protocone. Lower cheek teeth with entoconid completely incorporated in posterolophid, moderately wide buccal valley, longitudinal ectolophid, and no mesoconid and mesostylid; anteroposteriorly compressed and subrhomboidal m1 and m2 with long metalophid closing the trigonid basin posteriorly; m3 moderately expanded posteriorly,

with the metalophid failing to close the trigonid basin posteriorly. Enamel on the basin smooth.

**Differential diagnosis** Characters of the dentition clearly demonstrate that *Plesiosciurus* is a generalized sciurid. So far as the size and morphology are concerned, the genus shows some similarities to *Tamias*, *Sinotamias* and *Palaeosciurus* of the Neogene.

*Plesiosciurus* exhibits resemblance to *Tamias* in having short anteroloph in P4, complete and nearly converging protoloph and metaloph bearing no protoconule in M1 and M2, and subrhomboidal m1 and m2 with obscure entoconid and longitudinal ectolophid, but differs from the latter in: 1) the relatively heavily built teeth with more pronounced cusps than crests; 2) the P4-M2 having larger protocone and relatively lower lophs; 3) the entoconid completely incorporated in posterolophid in p4-m3; 4) the absence of mesostyle in P4-M2, and of mesoconid and mesostylid in p4-m2; 5) the lower molars having more developed metalophid.

*Plesiosciurus* resembles *Sinotamias* in having relatively heavily built teeth with converging protoloph and metaloph in M1 and M2, the entoconid completely merged with the posterolingual crest in p4-m3, the absence of mesostyle in upper molars, and of mesoconid and mesostylid in lower molars, but differs in having an anteroposteriorly expanded protocone and more complete metaloph in P4-M2, and a longitudinal ectolophid and a more developed metalophid in lower molars.

*Plesiosciurus* can be distinguished from *Palaeosciurus* by its relatively thin but complete metaloph in P4-M2, lack of a distinct entoconid, a mesoconid and a mesostylid in p4-m2.

***Plesiosciurus sinensis* Qiu & Lin, 1986**

(Fig. 3)

*Spermophilinus* sp.: Li et al., 1983, p. 313

**Holotype** Right M1/2 (IVPP V 8157 from Songlinzhuang).

**Paratypes** One left mandibular fragment with damaged m2 and m3, seven cheek teeth (3 M1/2, 1 p4, 2 m1/2, 1 m3 from Songlinzhuang), V 8158.1-8.

**Referred specimens** Shuanggou: one m1/2 and one m3, V 8158.9-10. Zhengji: six cheek teeth (1 DP4, 1 P4, 3 m1/2, 1 m3), V 8158.11-15, 17.

**Diagnosis** Same as for the genus.

**Description** The outline of the occlusal surface of the DP4 is subtriangular with expansion of parastyle and short anteroloph. The protocone is large and heavily built. The thin but complete protoloph and metaloph are nearly parallel as they join with the protocone. A protoconule is absent, but a prominent metaconule is present. A mesostyle is wanting. Both anteroloph and posteroloph are lower than the protoloph and the metaloph. The P4 is similar to the DP4 in structure, but larger and with stronger cusps and lophs. The outline of M1/2 is subquadrate with more pronounced cusps than lophs. The protocone is larger and slightly expanded anteroposteriorly. The protoloph and metaloph are low and thin, but complete. They are nearly convergent as they join the protocone, with the protoloph somewhat bulging just buccal of the protocone and the metaloph becoming constricted as it joins the base of



Fig. 3 Cheek teeth of *Plesiosciurus sinensis* from Sihong, Jiangsu in occlusal view

A. r DP4 (reversed, IVPP V 8158.11); B. r P4 (reversed, V 8158.12);  
C. r M1/2 (reversed, holotype, V 8157); D. I M1/2 (V 8158.4); E. r p4 (reversed, V 8158.5);  
F. I m1/2 (V 8158.6); G. I m1/2 (V 8158.14); H. r m3 (reversed, V 8158.10)

protocone. A protoconule is absent, but the metaconule is marked. A mesostyle is missing.

The p4 is distinctly narrower anteriorly than posteriorly with the protoconid and the metaconid situated very close to one another. The entoconid is incorporated in the posterolophid. A mesoconid and a mesostylid are absent. The m1/2 is subrhomboidal and compressed anteroposteriorly. The anteroconid is poorly developed. The entoconid is completely incorporated in the posterolingual crest connecting the metaconid with the hypoconid. The entoconid corner is curved. A mesoconid and a mesostylid are lacking. The anterolophid is low and joins the base of the protoconid. The posterolophid is more elevated than the anterolophid. The metalophid is long and connects the protoconid and metaconid to close the trigonid basin posteriorly. The buccal valley is moderately wide and the talonid basin is dammed by a nearly longitudinally arranged ectolophid. The m3 is moderately expanded posteriorly. The entoconid is completely incorporated in the posterolingual crest linking the metaconid and hypoconid. The ectolophid is distinct but bears no mesoconid. The metalophid fails to close the trigonid basin posteriorly. Enamel of the talonid basin of p4-m3 is smooth.

**Discussion** *Plesiosciurus sinensis* was considered to be an intermediate between chipmunks or ground squirrels and tree squirrels, and to have been evolved from the former, quite close to the point of its divergence (Qiu and Lin, 1986). After the present restudy, however, I believe the sciurid species possesses a combination of features that tend to set it off from tree squirrels. These significant characters are the pointed cusps and the relatively low

and thin crests, the subquadrate M1 and M2 with converging protoloph and metaloph, and the marked metaconule, the absence of entoconid and mesoconid in the subrhomboidal m1 and m2. This appears to suggest that *P. sinensis* belongs to a chipmunk or ground squirrel group. Therefore, the material described above is referred to the tribe Tamiini rather than Sciurini.

### ***Shuanggouia* Qiu & Lin, 1986**

**Type species** *Shuanggouia lui* Qiu & Lin, 1986.

**Emended diagnosis** Generalized sciurid with size close to *Sciurus*, and moderately elevated cusps and lophs. P4 larger than M1, with distinct and expanded parastyle and developed anteroloph; P4-M2 with slightly expanded protocone, complete and transverse protoloph bearing no protoconule, obliquely arranged and lingually constricted metaloph with marked metaconule, and the two lophs distinctly converging towards the protocone; M3 with remnant of metaconule and metaloph. Lower cheek teeth with entoconid nearly incorporated in posterolophid, narrow and shallow buccal valley, short ectolophid bearing small mesoconid, and distinct metaconid crest; subquadrate m1 and rhomboidal-subrectangular m2 with metalophid closing the narrow and high trigonid basin posteriorly; m3 distinctly expanded posteriorly, with a more pronounced mesoconid. Enamel on the basins showing irregular pattern of crests.

**Differential diagnosis** *Shuanggouia* resembles *Sciurus*, *Palaeosciurus* and *Aliveria* in size and in having complete protoloph and metaloph in P4-M2, and incompletely incorporated entoconid in lower cheek teeth. It differs from *Sciurus* in having more elevated cusps and crests, less expanded protocone and the protoloph and metaloph converging toward the protocone in P4-M3, distinct metaconule in P4-M2, less delimited entoconid in p4-m2. The main differences between *Shuanggouia* and *Palaeosciurus* are: 1) the P4 is larger than M1 in *Shuanggouia*, but smaller in *Palaeosciurus*; 2) *Shuanggouia* has a mesostyle and a short mesostyle crest in P4-M2, but a mesostyle crest is absent in *Palaeosciurus*; 3) in relation to m2, the m1 is longer than wide in *Shuanggouia*, but it is subquadrangular in outline in *Palaeosciurus*. *Shuanggouia* can be distinguished from *Aliveria*, a “flying squirrel” with dental pattern of a generalized sciurid by the larger P4 in relation to M1, the absence of hypocone, protoconule, or a double metaconule in P4-M2, and the weaker anteroconid or the absence of an entolophid in p4-m2.

### ***Shuanggouia lui* Qiu & Lin, 1986**

(Fig. 4)

*Miopetaurista* sp. II: Li et al., 1983, p. 327

Sciuridae gen. et sp. indet.: Qiu and Lin, 1986, p. 203

Sciuridae gen. et sp. indet.: Qiu and Qiu, 2013, p. 147

**Holotype** Left maxillary fragment with P3-M2 (IVPP V 8153 from Shuanggou).

**Paratypes** Three DP4 (V 8154.1-3), one P4 and one m3 (V 8152.8, 9) from Shuanggou and Songlinzhuang.

**Referred specimens** Songlinzhuang: one left mandibular fragment with broken incisor and p4-m2, seven cheek teeth (1 DP4, 1 P4, 1 M3, 4 m1/2), V 8154.7, 8, 11, 14, 15, 16, 18, 20. Zhengji: one M3, V 8154.21.

**Diagnosis** Same as for the genus.

**Description** The single-rooted P3 is bud-shaped, with a prominent main cusp and a low ridge encircling the posterolingual margin of the tooth. The outline of the occlusal surface of the DP4 is subtriangular, due to the prominent and expanded parastyle. The protocone is the largest among the main cusps, and has its longitudinal axis inclined anterointernal-posteroexternally. A hypocone is absent. The transverse protoloph and the oblique metaloph are complete and connected with the protocone, with the metaloph constricted at the protocone. There is no protoconule, but a distinct metaconule, a small mesostyle and a short mesostyle crest are present. The P4 is similar to the DP4, except for its subquadrangular outline due to the less expanded parastyle and long anteroloph, its larger size, and stronger cusp and lophs. The M1 is smaller than the P4, and longer buccally than lingually. The protocone is not much expanded anteroposteriorly. The protoloph and metaloph are complete, converging towards the protocone, with the metaloph slightly constricted just buccal of the protocone. A protoconule is absent, but a distinct metaconule is present. A small but delimited mesostyle and a short mesostyle crest are also present. The M2 is similar to the M1 in morphology, except for its subrectangular outline, relatively larger width than length, longer anteroloph and narrower anterior valley. The M3 is moderately expanded posteriorly. The protocone and protoloph are strong. Remnant of a metaloph and a metaconule are distinguishable. In the M3 its basin shows an irregular pattern of crests as in other little-worn M1 and M2.

The p4 is distinctly narrower anteriorly than posteriorly with the protoconid and the metaconid situated very close to each other. The entoconid is incorporated in the posterolophid. A mesoconid is indistinct and a mesostylid is absent, but a metaconid crest is present. The m1 is longer than wide. The entoconid is nearly incorporated in the posterolophid. The entoconid corner is curved. The mesoconid is small and the mesostylid is indistinct. The metaconid crest joins the metaconid. The trigonid basin is narrow and distinctly higher than the talonid basin. The buccal valley is narrow and shallow, with the talonid basin dammed by the short ectolophid. The m2 is similar to the m1, except for its larger size, subquadrangular outline, and angular entoconid corner. The m3 is distinctly expanded posteriorly. The mesoconid is relatively larger and the trigonid basin is lower than in the m1 and m2. The metalophid is connected with the metaconid. Enamel on the talonid basin is rugged as in p4-m2.

**Discussion** Some specimens previously published by Qiu and Lin (1986) from Sihong under the name *Shuanggouia lui* seem not to correspond in features with the holotype. They possess some characters that tend to be close to *Sciurus*, and have been rejected from the genus *Shuanggouia* and once were referred to *Sciurus* (see Qiu and Yan, 2005), but now to *Palaeosciurus* (see above). In addition, a damaged m2 (formerly considered m3) from Songlinzhuang, Sihong and assigned to an indeterminate Sciuridae by Qiu and Lin (1986)



appears to belong to *Shuanggouia lui*.

*Shuanggouia* was formerly grouped in *Petauristinae* and compared with *Aliveria*, a “flying squirrel” known from Evia, Greece (De Bruijn et al., 1980; Qiu and Lin, 1986). Despite their

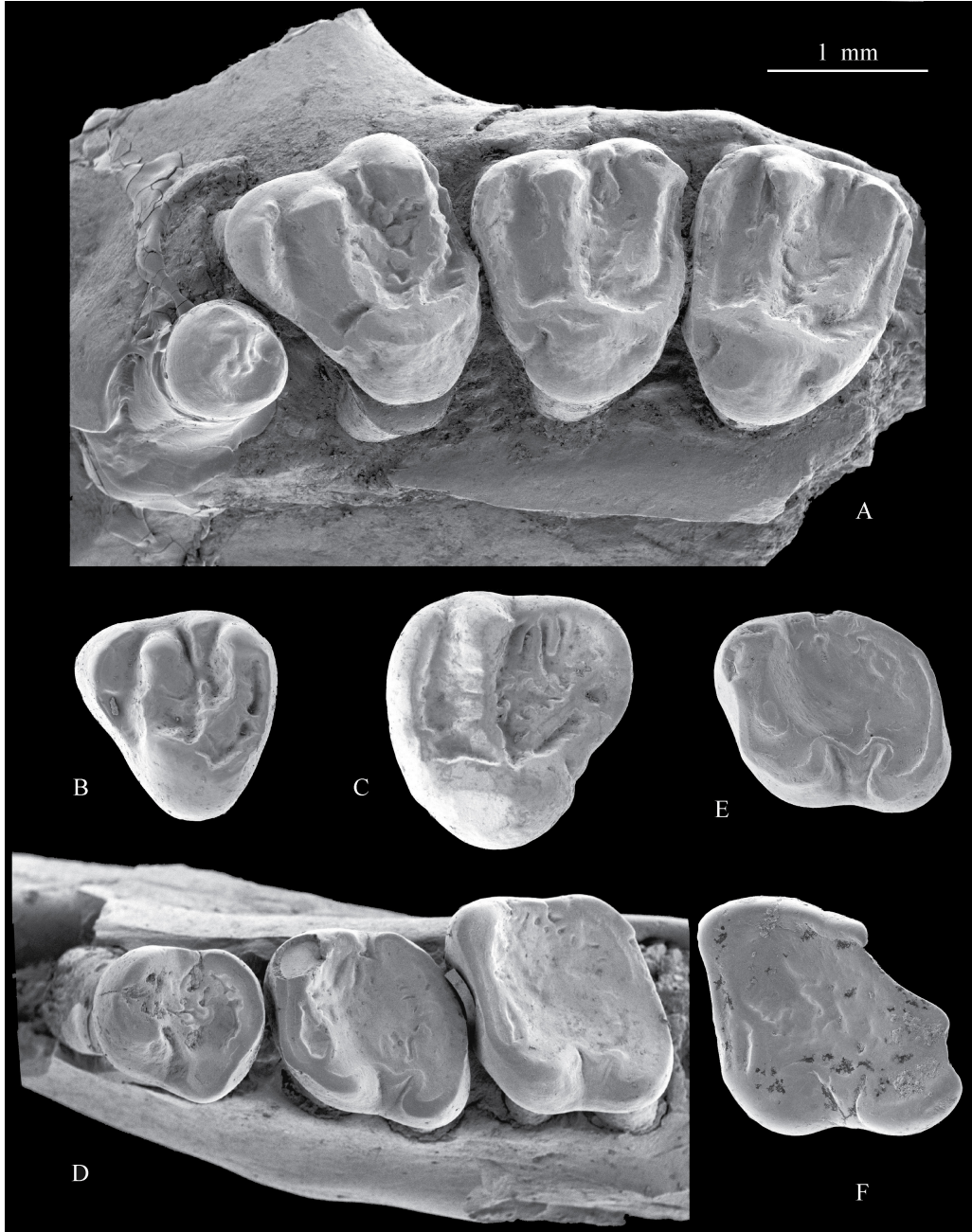


Fig. 4 Cheek teeth of *Shuanggouia lui* from Sihong, Jiangsu in occlusal view

A. left maxillary fragment with P3-M2 (holotype, IVPP V 8153); B. r DP4 (reversed, V 8154.1); C. r M3 (reversed, V 8154.11); D. left mandibular fragment with broken incisor and p4-m2 (V 8154.7); E. r m1/2 (reversed, V 8154.14); F. r m3 (reversed, V 8152.9)

differences, *S. lui* and species of *Aliveria* evidently share some common characters, such as the simple dental pattern with the unexpanded protocone situated anteriorly, the protoloph and metaloph converging toward the protocone, and a distinct metaconule and a free mesostyle present in P4-M2, a remnant of metaloph in M3, the partly merged entoconid in p4-m2, and the basins showing an irregular pattern of crests and cuspules. Nevertheless, the simple dental pattern, the absence of protoconule and the presence of metaconule in P4-M2, the indistinct entoconid in p4-m2 recall the dental pattern of *Shuanggouia* rather than that of a generalized sciurid. As mentioned above, *Shuanggouia* is similar to *Palaeosciurus* in dental morphology, especially the elevated cusps and crests, the convergence of protoloph and metaloph, and the lingually constricted metaloph with distinct metaconule in P4-M2, and the partly incorporated entoconid in p4-m2. The similarity of the two genera probably indicates that they can be included in the same tribe Tamiini.

### **Pteromyinae Brandt, 1855**

#### ***Parapetaurista* Qiu & Lin, 1986**

**Type species** *Parapetaurista tenurugosa* Qiu & Lin, 1986.

**Emended diagnosis** Flying squirrel with medium-sized and low-crowned cheek teeth. P4 with prominent and expanded parastyle; P4-M2 with protocone expanded anteroposteriorly, paracone distinctly larger than metacone, protoloph and metaloph relatively weak, nearly parallel in direction, and obliquely connected with protocone, protoconule and metaconule undeveloped, but a short protolophule present; less posteriorly expanded M3 without metaloph; p4-m2 with delimited entoconid, distinct mesoconid, angular entoconid corner, strong and elevated posterolophid; m1/2 with small mesostylid connecting to metaconid, complete metalophid, and distinct anterobuccal sinusid. Enamel surface in the basins showing crenulated pattern.

**Differential diagnosis** *Parapetaurista* is considered to be a medium-sized flying squirrel with the dental pattern closer to that of a generalized sciurid, and therefore distinguishable from large-sized sciurine genera whose molars show a complicated pattern and crenulated enamel surface, such as *Petaurista*, *Hylopetodon*, *Albanensia* and *Yunopterus*. The genus is also easily differentiated from *Aliveria*, *Pliopetaurista* and *Forsythia*, whose molars possess convergence of protoloph and metaloph in P4-M2.

*Parapetaurista* resembles *Miopetaurista*, *Petauristodon* and *Hylopetes* in having simpler dental pattern with parallel protoloph and metaloph in P4-M2. It differs from *Miopetaurista* in the smaller size, having more prominent protolophule in P4-M2, and more pronounced cusps, weaker mesoconid, mesostylid and anterobuccal sinusid in m1/2. The main differences between *Parapetaurista* and *Petauristodon* are: 1) a distinct hypocone and a metaconule are present in P4-M2 in *Petauristodon*, but absent in *Parapetaurista*; 2) the p4 is less molariform in *Parapetaurista* than in *Petauristodon*; 3) m1 and m2 have a more distinct mesoconid and an isolated mesostylid in *Petauristodon*, but both cusps are weak and the mesostylid is connected

with the metaconid in *Parapetaurista*. *Parapetaurista* is distinguishable from *Hylopetes* in larger size, having more elevated cusps and crests, distinctly larger paracone than metacone, more developed protolophule in P4-M2, and more conspicuous crenulation of the enamel surface in the basins.

***Parapetaurista tenurugosa* Qiu & Lin, 1986**

(Fig. 5)

*Miopetaurista* sp. I: Li et al., 1983, p. 313

**Holotype** Left M1/2 (IVPP V 8151 from Songlinzhuang).

**Paratypes** Seven cheek teeth (1 P4, 1 M3, 2 dp4, 1 p4, 1 m1/2, 1 m3 from Songlinzhuang), V 8152.1-7.

**Diagnosis** Same as for the genus.

**Description** The cheek teeth are low-crowned. The P4 is subrectangular in outline of the occlusal surface. The parastyle is prominent and slightly expanded. The protocone is pronounced and expanded anteroposteriorly. The paracone is distinctly larger than the metacone. The protoloph and metaloph are relatively weak but complete, nearly parallel, and connected with the protocone slightly obliquely. There is no sign of protoconule. A distinct metaconule is absent, but the middle part of the metaloph is bulged. A tiny mesostyle, a short protolophule, and a mesostyle crest can be observed. The M1/2 is rectangular and wider than long. The anteroposteriorly elongated protocone is the largest among the main cusps. The paracone is distinctly larger and higher than the metacone. The protoloph and metaloph are low, complete but constricted just buccal of the protocone. They are approximately parallel ridges connecting obliquely with the protocone. There is no distinct protoconule and metaconule. A mesostyle is absent. The protolophule is pronounced, extending buccally to one third of the central valley. The M3 is not very much expanded posteriorly. The protoloph is strong and the metaloph is absent. Enamel surface in the basin is crenulated as it is in M1/2.

The p4 is elongated, distinctly narrower anteriorly than posteriorly. The smaller protoconid and the larger metaconid are situated near one another, but are separated anteriorly by a deep valley and connected posteriorly by a short metalophid. A small anteroconid connected with the metaconid is present. The entoconid is prominent and the entoconid corner is angular. The mesoconid is small and the mesostylid is absent. The posterolophid is strong and very elevated. A small valley between the posterolophid and the hypoconid and a distinct crest between the protoconid and the ectolophid are present. The dp4 is similar to the p4, except for its small size and weak development of cusps and crests. The m1/2 is subrhomboidal with strong cusps and relatively low crests. The entoconid is delimited, connected with the distinct posterolophid and separated from the mesostylid by a notch. The entoconid corner is angular. The mesoconid is distinct. The mesostylid connecting to the metaconid is small. The anterolophid is strong. There is an anterobuccal sinusid between the anterolophid and the protoconid. The metalophid is low but connects the protoconid with the metaconid. The buccal



Fig. 5 Cheek teeth of *Parapetaurista tenurugosa* from Sihong, Jiangsu in occlusal view  
A. r P4 (reversed, IVPP V 8152.1); B. l M1/2 (holotype, V 8151); C. l M3 (V 8152.2); D. l dp4 (V 8152.4);  
E. r p4 (reversed, V 8152.5); F. l m1/2 (V 8152.6); G. r m3 (reversed, V 8152.7)

valley is wide and the talonid basin is dammed by a weak ectolophid. The m3 is distinctly expanded posteriorly. The entoconid is not well delimited and separated from the mesostylid by a notch. The mesoconid and the mesostylid are relatively more prominent than in m1/2. The metalophid is thick, but fails to close the trigonid posteriorly. As in p4 and m1/2, the basin shows irregular wrinkled surface.

**Discussion** The described specimens are close to those of *Shuanggouia lui* and *Palaeosciurus jiangi* in size, but can be referred to neither species, differing from them mainly in having parallel protoloph and metaloph, and in the presence of a distinct protolophule in P4 and M1/2, a more conspicuous entoconid and mesoconid in p4 and m1/2, and the less robust wrinkled enamel in the basins. A combination of features, i.e. the presence of distinct protolophule in M1/2, prominent entoconid, mesoconid and anterobuccal sinusid in m1/2, and the rugose enamel in the basins, appears to demonstrate that *Parapetaurista tenurugosa* is a flying squirrel. Molars of the taxon show a simpler pattern and a peculiarly crenulated enamel surface, similar to those of *Miopetaurista* and *Hylopetes* from Asia and *Petauristodon* from North America.

### 3 Concluding remarks

After the revision and supplementary description, the Sihong sciurid association is reallocated to five genera and species in two subfamilies, i.e. *Palaeosciurus jiangi*,

*Heterotamias sihongensis*, *Plesiosciurus sinensis* and *Shuanggouia lui* of Sciurinae, and *Parapetaurista tenurugosa* of Pteromyinae. The genus *Shuanggouia* previously placed in Petauristinae is transferred to the Sciurinae. A new genus *Heterotamias* is assigned based on the material formerly published under the name *Eutamias sihongensis*. Some specimens in *Shuanggouia* are referred to *Palaeosciurus*.

In composition, chipmunk-like sciurids seem to be a relatively abundant group in terms of species, as well as in terms of specimens. The true tree squirrels and flying squirrels are rare, and the ground squirrels are absent. This situation appears to imply that the Sihong sciurid assemblage is different from other sciurid faunas of the Miocene in China. The Shanwang association found in Shandong is dominated by tree squirrels, suggesting a forest biotope (Qiu and Yan, 2005). The faunas from Nei Mongol and Xinjiang are dominated by chipmunks and ground squirrels, indicating an environment of temperate arid steppe (Qiu, 1996; Meng et al., 2006; Wei, 2010; Qiu et al., 2013). Dominance of tree squirrels and flying squirrels in Lufeng and Yuanmou of southern China reflects a rather humid and forested environment of a tropical/subtropical habitat (Qiu, 2002; Qiu and Ni, 2006). Thus, the composition of the Sihong sciurid association seems to display an unusual palaeoecological environment of the Sihong area during the Early Miocene, which is neither a forest biotope nor an arid steppe, but something in between.

Most genera in the association are endemic to eastern China, representing relatively old known record of squirrels. *Heterotamias sihongensis* was formerly considered a rather primitive *Eutamias*/*Tamias*. The contemporaneous occurrence of *Heterotamias* in Sihong and *Tamias* in Nei Mongol seems to affirm that they are two independent lineages, and to suggest that they have derived from the same ancestral stock of sciurids in the Oligocene. Nevertheless, high endemism of the fauna and poor knowledge of phylogenetic relations for these animals make it difficult to compare with other faunas. Furthermore, some Sihong sciurids are still problematic. Such as, *Parapetaurista* exhibits dental characteristics intermediate between generalized sciurids and *Miopetaurista* or *Hylopetes*. Whether this Early Miocene flying squirrel is related to *Miopetaurista*, or even with Middle–Late Miocene representatives of pteromyines is still uncertain. A correct interpretation of the Sihong association would therefore await further collection and more complete evidence.

**Acknowledgements** The author would like to express his gratitude to Dr. X M Wang from the Natural History Museum of Los Angeles County, USA, Dr. L J Flynn from Harvard University, USA, and Z Q Zhang from IVPP for commenting on the manuscript and English content. Many thanks are also due to Miss H W Si and Mr. W D Zhang from IVPP for the photographs.

## 江苏泗洪早中新世松鼠类化石的补充描述与修订

邱铸鼎

(中国科学院古脊椎动物与古人类研究所 北京 100044)

**摘要:** 重新研究了中国发现较早、种类较多的江苏泗洪松鼠化石组合。基于对化石松鼠类的最新知识, 这些采自下中新统下草湾组的标本被重新鉴定和补充描述, 对原拟定为新属和新种的鉴别特征做了修改。原先指定为*Eutamias*的属被改名为*Heterotamias*新属; 归入鼯鼠亚科的*Shuanggouia*属被确定为松鼠亚科; *Shuanggouia lui*中的一些标本被认为与正模的形态特征不符而被指定为*Palaeosciurus*属。经重新研究, 这一组合被订正为*Palaeosciurus jiangi*, *Heterotamias sihongensis*, *Plesiosciurus sinensis*, *Shuanggouia lui*和*Parapetaurista tenurugosa* 5种。其中*Parapetaurista*属与中新世中、晚期的*Miopetaurista*较相似, 但它们的系统关系仍难以确定。研究表明, 泗洪松鼠化石组合似乎是一个组成上以类花栗鼠为主、分布局限于中国东部地区的地方性动物群。

**关键词:** 江苏泗洪, 早中新世, 下草湾组, 松鼠科

**中图法分类号:** Q915.873      **文献标识码:** A      **文章编号:** 1000-3119(2015)03-0219-19

### References

- Daxner-Höck G, 1998. Säugetiere (Mammalia) aus dem Karpat des Korneuburger Beckens. 3. Rodentia und Carnivora. Beitr Paläont, 23: 367–407
- Daxner-Höck G, 2003. Mammals from the Karpatian of the Central Paratethys. In: Brzobohaty R, Cicha I et al. eds. The Karpatian – A Lower Miocene Stage of the Central Paratethys. Brno: Masaryk University. 293–310
- De Bruijn H, 1998. Vertebrates from the Early Miocene lignite deposits of the opencast mine Oberdorf (western Styrian Basin, Austria): 6. Rodentia I (Mammalia). Ann Naturhist Mus Wien, 99A: 99–137
- De Bruijn H, Van der Meulen A J, Katsikatos G, 1980. The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece) – Part 1. The Sciuridae. Proc K Ned Akad Wet, Ser B, 83(3): 241–261
- Dehm R, 1950. Die Nagetiere aus dem Mittel-Miocen (Burdigalium) von Wintershof-West bei Eichstatt in Bayern. Neues Jahrb Miner Geol Paläont, Abh B, 91: 321–428
- Li C K, Lin Y P, Gu Y M et al., 1983. The Aragonian vertebrate fauna of Xiacaowan, Jiangsu. Vert PalAsiat, 21(4): 313–327
- Mein P, Ginsburg L, 2002. Sur l'âge relative des différents dépôts karstiques Miocènes de La Grive-Saint-Alban (Isère). Cah Sci Mus Hist Nat, Lyon, 2: 7–47
- Meng J, Ye J, Wu W Y et al., 2006. A recommended boundary stratotype section for Xiejian Stage from northern Junggar Basin: implications to related bio-chronostratigraphy and environmental changes. Vert PalAsiat, 44(3): 205–236
- Qiu Z D, 1996. Middle Miocene micromammalian fauna from Tunngur, Nei Mongol. Beijing: Science Press. 1–216
- Qiu Z D, 2002. Sciurids from the Late Miocene Lufeng hominoid locality, Yunnan. Vert PalAsiat, 40(3): 177–193

- Qiu Z D, Lin Y P, 1986. The Aragonian vertebrate fauna of Xiacaowan, Jiangsu. 5. Sciuridae (Rodentia, Mammalia). Vert PalAsiat, 24(3): 191–205
- Qiu Z D, Ni X J, 2006. Small mammals. In: Qi G Q, Dong W eds. *Lufengpithecus hudienensis* Site. Beijing: Science Press. 113–130
- Qiu Z D, Qiu Z X, 2013. Early Miocene Xiejiahe and Sihong fossil localities and their faunas, eastern China. In: Wang X M, Flynn L J, Fortelius M eds. Fossil Mammals of Asia. New York: Columbia University Press. 142–154
- Qiu Z D, Yan C L, 2005. New sciurids from the Miocene Shanwang Formation, Linqi, Shandong. Vert PalAsiat, 43(3): 194–207
- Qiu Z D, Wang X M, Li Q, 2013. Neogene faunal succession and biochronology of central Nei Mongol (Inner Mongolia). In: Wang X M, Flynn L J, Fortelius M eds. Fossil Mammals of Asia. New York: Columbia University Press. 155–186
- Vianey-Liaud M, 1974. *Palaeosciurus goti* n. sp., écureuil Terrestre de l'Oligocène moyen du Quercy. Données nouvelles sur l'apparition des sciuridés en Europe. Ann Paléont, 60(1): 103–122
- Wei Y P, 2010. *Atlantoxerus* from the Middle Miocene of northern Junggar Basin and their environmental significance. Vert PalAsiat, 48(3): 220–234
- Ziegler R, Fahlbusch V, 1986. Kleinsäuger-Faunen aus der basalen Obern Süßwasser-Molasse Niederbayerns. Zitteliana, 14: 3–80